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# What you see depends on what you saw, and what else you saw: The interactions between motion priming and object priming

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ABSTRACT

Both visual object priming and motion priming have been reported independently, but the interactions between the two are still largely unexplored. Here we investigated this question using a novel type of SFM stimuli, 3-D helixes, and found that the motion direction perception of an ambiguous helix can be biased by the motion direction of a preceding SFM stimulus – a classic motion priming effect. However, the effectiveness of motion priming depends on object priming: a neutral object priming produced a weak motion priming, a congruent object priming led to a strong motion priming, and critically, an incongruent object priming abolished and overpowered the motion priming. In contrast, object priming alone (in the absence of motion overlap) had little effects biasing motion perception. Taken together, these results suggest that there exists an integrated neural representation of motion and structure of 3-D SFM stimuli, and motion priming of 3-D SFM stimuli might happen at an intermediate stage between MT/V5 (which is not shape selective) and LO (lateral occipital, which is not motion selective). This novel type of stimuli, 3-D helixes, along with the prime–target paradigm, thus might offer a unique tool to examine neural bases underlying the perception of 3-D SFM stimuli and perceptual priming.



## 1. Introduction

What we perceive at any given moment is influenced by what we just saw or heard, particularly when the current object is ambiguous, a phenomenon known as perceptual priming (Grill-Spector, Henson, & Martin, 2006; Schacter, Wig, & Stevens, 2007; Wiggs & Martín, 1998). For example, people typically perceive an ambiguous rabbit–duck picture (target) as a rabbit if it is preceded by an unambiguous picture of a rabbit (prime), and vice versa. Also, a target 3-D object whose direction of rotation is ambiguous (due to the lack of depth cues) is often perceived as rotating in the same direction when preceded by an unambiguously rotating 3-D prime (e.g., Jiang, Pantle, & Mark, 1998; Nawrot & Blake, 1993).

Such perceptual priming effects have typically been *independently* examined for different stimulus features, such as shape (e.g., Humphreys & Quinlan, 1988) and motion (e.g., Anstis & Ramachandran, 1987; Pinkus & Pantle, 1997). Evidence from neuroimaging and transcranial magnetic stimulation (TMS) studies also generally suggests that perceptual priming of object shape/structure involves regions in the ventral visual pathway (Jiang et al., 2007; Kourtzi & Kanwisher, 2001), whereas motion priming is due to modified neuronal responses in area MT/V5 (or the human analogue of middle temporal cortex, hMT+) of the dorsal pathway (Ashida et al., 2007; Brascamp et al., 2010; Campana, Cowey, & Walsh, 2002; Jiang, Luo, & Parasuraman, 2002). Moreover, perceptual priming (or sometimes referred as adaptation) has been used as a tool to examine the neural representations of specific object classes and/or features (Grill-Spector, Henson, & Martin, 2006; Schacter, Wig, & Stevens, 2007). For example, changes in face shapes led to modulations of neuronal responses at fusiform face area (FFA) – a critical region of face processing (Kanwisher, McDermott, & Chun, 1997), but not early visual cortices, suggesting face shapes may be encoded by neurons in FFA, but not the neurons in early visual cortices (Jiang et al., 2006); and changes of words but not the case of words led to modulations of neuronal responses at visual word form area (VWFA) – a critical region of reading (McCandliss, Cohen, & Dehaene, 2003), suggesting that neurons at VWFA are selective to words, but not the word cases (Dehaene et al., 2001).

In the present study, we used perceptual priming (with a 100 ms brief interval between the prime and target SFM stimuli) as a tool to investigate the processing of 3-D SFM (structure-from-motion)

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stimulus. More specifically, we test whether the representations of motion direction and object structure of 3-D SFM stimuli are largely independent from each other, or tightly integrated with each other. For instance, with a longer interval between the prime and target stimuli (>1 s), while some previous studies have suggested that motion priming was unaffected by changes of color or shape between prime and target (e.g., Chen & He, 2004; Maier et al., 2003) – suggesting separated neural representations of the motion and object structure of an SFM stimulus, a very recent study has revealed reduced motion priming when the prime and target stimuli constituted different objects (Pastukhov, Füllekrug, & Braun, 2013) – suggesting a rather integrated neural representation for the motion and object structure of a 3-D dynamic object. To further complicate the scenario, a very recent study of motion aftereffect has found that negative motion aftereffect is shape irrelevant (Pastukhov, Lissner, & Braun, 2014). Resolving this controversy can therefore advance understanding of the neural mechanisms underlying the recognition of moving 3-D objects (Kourtzi & Connor, 2011; Orban, 2011; Todd, 2004). Furthermore, it is unknown (to the best of our knowledge) whether object priming and motion priming can be observed simultaneously, and if so, how the two priming effects interact with each other.

Here we aimed to address this controversy and investigated the interactions between motion priming and object priming using a novel structure-from-motion (SFM) stimulus, a 3-D helix rotating around *Y*-axis, with a prime–target paradigm with a brief interval between the prime and target stimulus (100 ms). It is worth to note that recent studies have suggested a distinction between perceptual priming with a brief interval between the prime and target stimuli (e.g., 100 ms in the present study) and those with a longer interval (e.g., >1 s), the former is usually named neural persistence or inertia (Anstis & Ramachandran, 1987), while the later is usually termed perceptual/sensory memory (Chen & He, 2004; Maier et al., 2003; Pastukhov, Füllekrug, & Braun, 2013). For instance, a mask image between the prime and target stimuli will disrupt neural persistence, but not sensory memory (Pastukhov & Braun, 2013). Nevertheless, both neural persistence/inertia (Jiang, Luo, & Parasuraman, 2002; Jiang, Pantle, & Mark, 1998; Nawrot & Blake, 1993; Pinkus & Pantle, 1997) and sensory memory (Brascamp et al., 2010; Chen & He, 2004; Maier et al., 2003; Pastukhov, Füllekrug, & Braun, 2013; Sterzer & Rees, 2008) have been widely used to investigate the processing of 3-D SFM stimulus. In addition, we were not aware of any priming studies with a brief interval (less than half second) have examined the relationship between motion priming and object structure. In the present study, we examined whether the perceived rotating direction of an ambiguous 3-D helix can be biased by the rotating direction of a preceding stimulus with a different object structure (e.g., no object cue) or a motion priming with a neutral object priming (Experiment 1), the object structure of a preceding stimulus in the absence of motion cue (Experiment 3), or both (in the presence of both motion and object cues) (Experiment 2). We hypothesized that, if there exists an integrated neural representation of the motion and object of an SFM stimulus, motion priming would be significantly influenced by object priming; by contrast, if the motion and object information of an SFM stimulus are encoded by disjointed populations of neurons, the motion priming and object priming should have very limited influence on each other.

## 2. General methods

### 2.1. Helixes

Two types of 3-D spatial structures, left-handed and right-handed helixes, were developed (Fig. 1). One was a mirror image of the other. A set of 150 dots was randomly (normal distribution) chosen from the 2-D orthogonal projection of a helix (5.5° × 11°) with (Fig. 2A) or without depth cues (Fig. 2B). Two types of depth cues were used: luminance and size. The dots that were closer to participants had higher luminance (1:4) and were larger (1:3) than those that were farther. Previous studies (e.g., Dosher, Sperling, & Wurst, 1986; Jiang, Pantle, & Mark, 1998) have found that these two types of cues (size and luminance) provide sufficient depth information, and subjects could perceive an unambiguous rotation direction correctly. The common fate of the dots' local motion (left vs. right) generated the perception of a global rotating 3-D helix. When displayed with depth cues, both the perceived structure and rotating direction of the helix were unambiguous (Fig. 2A). In contrast, when displayed without depth cues, like many other such stimuli (e.g., cylinder, sphere, etc.) used in other previous studies, the rotating direction of the 3-D helix around the *Y*-axis was ambiguous, and could be perceived as either clockwise or counterclockwise with equal probability. More importantly, *the 3-D helix had an important and unique feature that many other stimuli do not have, namely, its 3-D structure was also ambiguous, and the perceived 3-D structure was bound with the perceived 3-D rotating direction* (Fig. 2B). Such a unique feature provides the opportunity to bias the perception of 3-D helixes through a motion cue, or an object cue, or both, and to investigate the interactions between motion and object priming.

In the present study, the 2-D projection of the 3-D helix was displayed against a totally dark background. During the experiment, the 3-D helix would rotate for twenty pages around the *Y*-axis at speed of 5° per page in either a clockwise or counterclockwise direction, and each page stayed on the screen for two frames (about 33.3 ms) (the same speed and stimuli duration were used to present all stimuli rotating around the *Y*-axis). The set of dots were pseudo-randomly chosen for each trial separately to avoid long-term low-level adaptation. In all three experiments, 3-D helixes rotating around the *Y*-axis in the absence of depth cues were used as the target stimuli. For all stimuli (prime or target), a set of 150 dots was randomly (normal distribution) chosen from the 2-D orthogonal projection of corresponding object structures with or without depth cues. The same depth cues were used for all stimuli in three experiments. The visual angles of all stimuli were about 5.5° × 11° (viewing from a distance of 57 cm).

### 2.2. Apparatus

A Gateway Pentium-II personal computer with a Sony G220 17" monitor (refresh rate 60 Hz, brightness and contrast at 50% and 100% respectively) was used. A gray board with a square hole

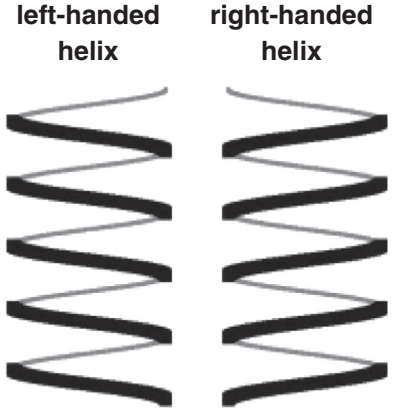


**Fig. 1.** Two basic types of helixes.

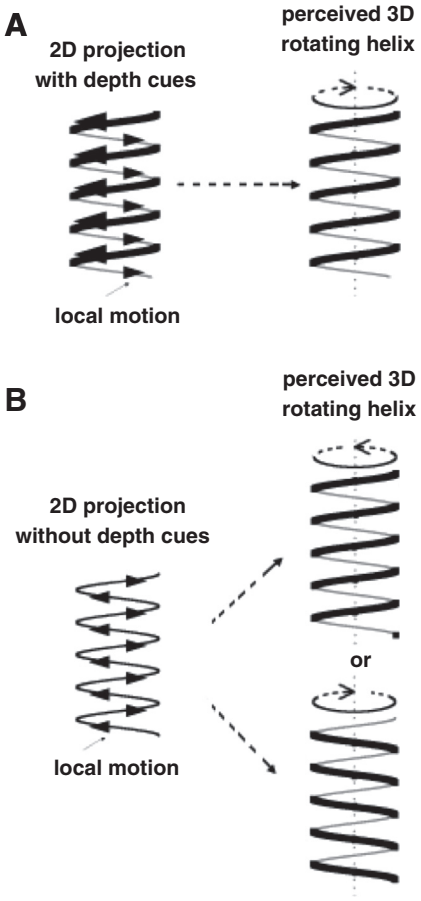


**Fig. 2.** The perception of a rotating (around *Y*-axis) helix from its 2-D projection. (A) When the 2-D projection has depth cues, the perceived rotation direction and 3-D structure are both unique; (B) when the 2-D projection does not have depth cues, both rotation direction and 3-D structure are ambiguous, and the perceived rotation direction and perceived 3-D structure are tied to each other.

($16° \times 16°$) was put in front of the computer monitor so that only the center of the monitor was visible to the participants. Participants viewed all stimuli at a distance of 57 cm. The same equipment and settings were used for all three experiments.

### 2.3. Participants

Undergraduate and graduate students (aged from 18 to 26) from local colleges participated in the study. All had normal or corrected-to-normal visual acuity. A signed consent form was obtained prior to participating in the study and the research was conducted in accord with the Code of Ethics of the World Medical Association (Declaration of Helsinki). In the three experiments, data from a total of nine subjects were excluded, including those unable to perceive the 3-D structure ($n = 4$) or being able to perceive only one rotating direction ($n = 5$). In the end, data from nine (Experiment 1), eight (Experiment 2), and seventeen (Experiment 3) participants were included in the data analysis. The rationale for more subjects in Experiment 3 is that there were fewer trials per condition (half of those in Experiment 1 and 2).

### 2.4. Procedure and design

Each participant perceived 288 trials in nine blocks. A fixation cross always came out 500 ms before the onset of the first (prime) stimulus, and it stayed on the screen until the end of each trial. The next trial started 5 s after the end of the current trial.

In one of nine blocks, a single ambiguous helix was displayed without depth cues. The participants' performance data were used to set up a baseline for motion direction perception in absences of any depth cue. Based on the data from previous studies (Jiang, Pantle, & Mark, 1998), we predicted that the motion direction of the 3-D helix should be perceptually ambiguous.

The trials in the other eight blocks had two visual stimuli displayed successively. The first one was a structure-from-motion (SFM) stimulus with depth cues (the size and luminance of dots): a rotating cylinder or a set of rotating circles in Experiment 1, a helix rotating around *Y*-axis in Experiment 2, or a static helix or a helix rotating around *X*-axis in Experiment 3. The second (target) stimulus was always a 3-D helix rotating around *Y*-axis in absence of depth cues. There was a 100 ms delay between the offset of the first stimuli and the onset of the second stimuli. Participants were asked to passively view the first stimulus and judge the motion direction of the second stimulus (a 3-D helix without depth cues) as accurately and soon as possible. Participants were tested with a few trials to make sure these depth cues (luminance and dot size) were sufficient for them to perceive the designed depth in this study.

## 3. Experiment 1

### 3.1. Introduction

Previous studies have found that the motion direction perception of an ambiguous 3-D rotation can be strongly biased by a preceding unambiguous 3-D rotation (e.g., Eddy & Holcomb, 2011; Jacobs & Fine, 1999; Jiang, Luo, & Parasuraman, 2002; Jiang, Pantle, & Mark, 1998; Nawrot & Blake, 1993). While prime and target stimuli that have the same object structure/shape have been used in most previous studies (but see Maier et al., 2003; Pastukhov, Füllekrug, & Braun, 2013), here using the classic prime–target paradigm, we investigated whether the motion perception of an ambiguous SFM helix can be biased by a preceding SFM stimulus with different object structures (a cylinder or a set of circles).

### 3.2. Methods

Two types of SFM stimuli, Cylinder or Circles (a set of circles), both rotating around the *Y*-axis in the presence of depth cues, were used as the prime stimuli in Experiment 1. A rotating cylinder has been used in several previous studies and has been demonstrated to be an appropriate type of SFM stimulus (e.g., Bradley, Chang, & Andersen, 1998). Meanwhile, the set of rotating circles were used to provide an alternative type of SFM stimuli because they yielded weaker motion perception and were more similar to the novel stimuli (rotating 3-D helixes) that were used as the target stimuli in this study. Because there was a non-informative object cue (cylinder or circles as the prime and helixes as the target stimuli), we also referred to this condition as the neutral object priming condition, in contrast to the congruent and incongruent object priming conditions in Experiment 2.

### 3.3. Results

When a helix rotated around the *Y*-axis without depth cues, its rotating direction was perceptually ambiguous, and could be perceived in a clockwise (CW) or counter-clockwise (CCW) direction. On average, participants perceived these ambiguous helixes rotating in the CW direction in about 52% (SEM = 10%) of trials, which was not significantly different from chance level ($p > 0.5$).

In contrast, when ambiguously rotating helixes were preceded by an unambiguously rotating cylinder or a set of circles, participants were more likely to perceived the helix as rotating in the same direction as the preceding stimuli (mean = 69.9%, SEM = 6.9%, $p < 0.04$, one-sample $t$-test) (Fig. 3), and there was no significant difference between the two priming conditions ($p > 0.3$, two-tailed $t$-test).

These results show that for a novel type of visual stimuli, rotating 3-D helixes, a motion priming effect was found when an ambiguous rotating 3-D helix was preceded by unambiguous 3-D rotating stimuli (either rotating cylinder or rotating circles). However, the priming effect was relatively weak (participants only perceived the ambiguous helixes rotating in the same direction as the prime stimuli on about 70% of trials) compared to previous reports that found motion priming on more than 90% of trials with a short ITI (intertrial interval) comparable to the one in the present study (100 ms)) (e.g., Jiang, Pantle, & Mark, 1998). The relatively weak motion priming effect might be due to the weak 3-D perception with helixes compared to other object structures (e.g., cylinders), or the difference in object structures between the prime (cylinders or circles) and target stimuli (helixes) (Pastukhov, Füllekrug, & Braun, 2013; but see Maier et al., 2003), despite the brief interval between the prime and target stimuli used in Exp. 1.

## 4. Experiment 2

### 4.1. Introduction

Motion priming has been proposed to be independent of information from other modalities, including shape and/or color (Chen & He, 2004; Maier et al., 2003), in line with findings from single-unit recording, neuroimaging, and transcranial magnetic stimulation (TMS) studies, which have suggested that MT/V5 (or the human analogue of hMT+) is the central region responsible for the phenomena of motion priming, due to altered response characteristics of *motion-selective* neurons in MT/V5 (or the human analogue of hMT+) (Ashida et al., 2007; Brascamp et al., 2010; Campana, Cowey, & Walsh, 2002; Jiang, Luo, & Parasuraman, 2002). In contrast, a recent study has proposed that motion priming of SFM stimuli might be shape specific, as a reduced motion priming is found when the prime and target SFM stimuli have different object structures (Pastukhov, Füllekrug, & Braun, 2013), suggesting that the relatively weak motion priming found in Experiment 1 might be due to the difference in object structure between the prime (helixes) and target (cylinders or circles) SFM stimuli, despite the difference in the duration of prime–target interval between the present and previous studies (Chen & He, 2004; Maier et al., 2003; Pastukhov, Füllekrug, & Braun, 2013).

However, to the best of our knowledge, there is no study that has directly investigated the interactions between object priming and motion priming—that is, whether the rotation direction of an ambiguous SFM stimulus (e.g., helix) can be biased by both the rotating direction and the object structure of a preceding SFM stimulus at the same time, when the two priming effects are congruent or incongruent with each other, and what the final perceived outcome is. In particular, is the motion direction or object structure of the prime stimulus more likely to decide the motion perception of the target stimulus? If the motion and object structure of an SFM stimulus are represented by two disjointed populations of neurons (e.g., motion at MT/V5, and object structure at lateral occipitotemporal region (LO)), motion priming should dominate and subjects would be more likely to perceive the ambiguous target stimuli rotating in the same direction as the preceding unambiguous stimuli. In contrast, if there are neurons that are selective to both the motion and object structure of an SFM stimulus and are involved in the processing of SFM stimuli, we would observe a strong competition between object priming and motion priming, with the final perception depending on the outcome of the competition between object priming and motion priming. Here we tested the two hypotheses using two priming conditions, congruent (Fig. 4A) and incongruent (Fig. 4B).

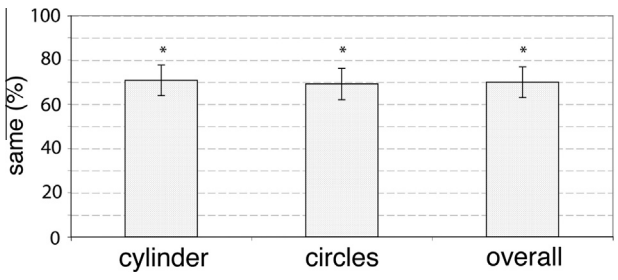


**Fig. 3.** Results of Experiment 1. Subjects perceive the ambiguous 3-D helixes rotating mostly in the same direction of the preceding unambiguous rotating cylinders or circles. *Represents $p < 0.05$. Error bars represent SEM.

### 4.2. Methods

3-D helixes with depth cues rotating around the *Y*-axis were used as the prime stimuli in Experiment 3. The motion direction perception of target 3-D helixes could therefore be primed by both the motion and object structure of the preceding prime stimuli. Critically, the two priming effects could be the same – called the *congruent condition* (Fig. 4A), or different – the *incongruent condition* (Fig. 4B). It should be noted that the last frame of the prime helixes was always presented at a position different to the first frame of target helixes to avoid potential low level priming or other potential confounding effects (see Experiment 3). In an additional block, a single helix was displayed with a depth cue to confirm that participants ($n = 7$) could reliably judge the rotating direction (defined by the depth cues) of a 3-D helix.

### 4.3. Results

Similar to the results in Experiment 1, the perception of motion direction of a single helix that rotated around the *Y*-axis without depth cues was ambiguous. Overall, subject perceived the ambiguous helix to rotate in the clockwise direction on 57% (SEM = 12%) of trials, which was not significantly different from chance level ($p > 0.4$). In contrast, when a single rotating 3-D helix was displayed with depth cues, participants always perceived the direction defined by depth cues (100%).

When the ambiguous helix (target) was preceded by an unambiguous one (prime), a one-sample $t$ test indicated that participants perceived the ambiguous target helix rotating in the same direction as the unambiguous prime under the congruent condition significantly more frequently than chance (86.4%, SEM = 2%, $p < 0.0000005$), but not under the incongruent condition, in which participants tended to perceive the ambiguous target helix rotating in the opposite direction of the unambiguous prime (41.7%, SEM = 5.1%, $p = 0.15$), suggesting a significant influence from the object structure of the prime stimulus on the motion direction perception of the target ambiguous stimulus (Fig. 4C). A paired $t$-test also indicated that the responses between the two conditions differed significantly ($p < 0.00004$). Furthermore, participants were faster to perceive the rotating direction of the ambiguous target in the congruent condition (RT = 1242 ms, SEM = 261) than in the incongruent condition (RT = 1365 ms, SEM = 280), $p < 0.009$ (two tailed $t$-test), suggesting a delay in processing SFM stimuli due to the conflict between the object priming and motion priming (Fig. 4D). Notably, in the incongruent condition, participants responded faster when their perceived motion direction was the

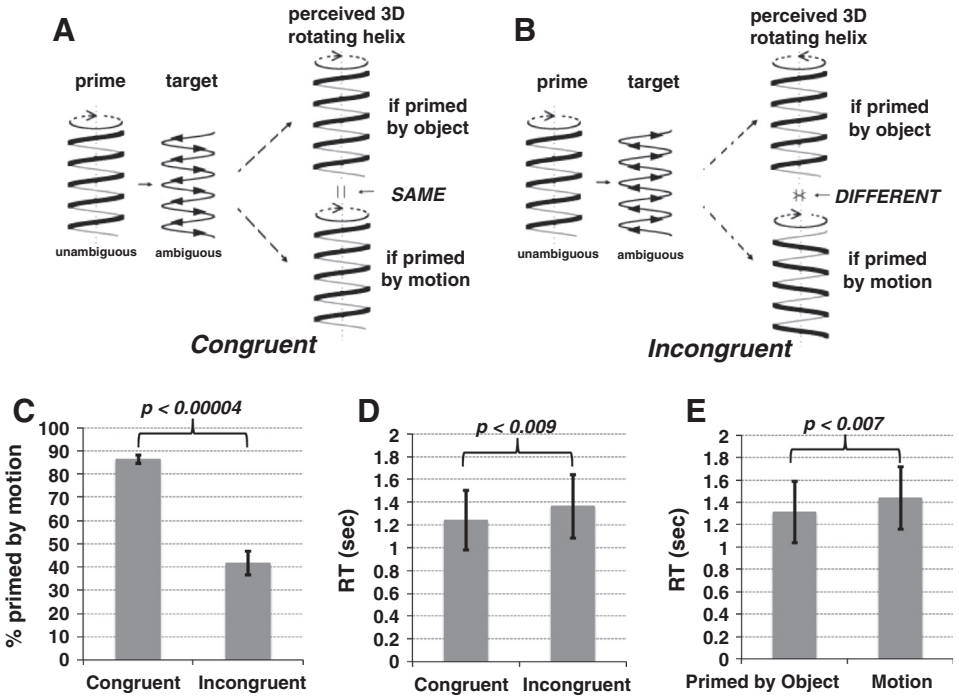


**Fig. 4.** Experiment procedure and conditions of Experiment 2. Two successive rotating helixes were displayed with a 100 ms ISI (interstimulus interval). The first one was displayed with depth cues, while the second one without. If the perception of the second rotating ambiguous helix could be biased/primed by both the motion direction and object structure of the first unambiguous one, then the two priming effects could be: (A) same – the *congruent condition*; or (B) different – the *incongruent condition*. (C) Motion priming was significantly stronger under the congruent than incongruent condition. (D) Subjects were faster in perceiving the motion direction of ambiguous helix under the congruent than incongruent condition. (E) Under the incongruent condition, subjects were faster in responding when their motion direction perception was primed by object than motion direction of the prime helix. Error bars represent SEM.

same as the one following the object structure (RT = 1312 ms, SEM = 274) than the motion direction of the unambiguous prime (RT = 1440 ms, SEM = 280) ($p < 0.007$, two-tailed $t$-test), suggesting a weak dominance of object priming over motion priming (Fig. 4E).

Contrary to the hypothesis that motion priming would dominate, the results in the incongruent condition revealed a strong competition between object priming and motion priming, i.e., a delay in perceiving the motion direction and abolished motion priming. Even more strikingly, incongruent object priming overpowered motion priming: participants tended to perceive the ambiguous helixes rotating in the same direction defined by the object structure but not the motion direction of the prime unambiguous helixes. Furthermore, participants were faster when they perceived the ambiguous target helixes rotating in the same direction defined by the object structure than by the motion direction of the prime unambiguous helixes. These results demonstrate for the first time strong interactions between the motion priming and object priming, and provide behavioral evidence supporting an integrated neuronal representation of both object structure and motion of SFM stimuli. However, one alternative explanation is that the interactions between motion priming and object priming might be due to a potential top-down feedback from the shape-selective neurons in the ventral pathway to motion-selective neurons in MT/V5. We examined this alternative hypothesis in Experiment 3 with prime stimuli that shared object structure but not the motion of the target stimuli.

## 5. Experiment 3

### 5.1. Introduction

The majority of perceptual priming studies have focused on within-modality priming, i.e., how motion perception can be affected by the motion direction of a preceding stimulus (e.g., Jiang, Pantle, & Mark, 1998). However, recent results from neuroimaging and animal studies have suggested strong interactions between the perception of object shape and motion (Kourtzi, Krekelberg, & van Wezel, 2008). Further supporting evidence of interaction provided by the strong anatomical connections and cross-talk between the ventral (mainly involved in the processing of shape information) and dorsal (mainly involved in the processing of motion and space information) visual pathways (Haxby et al., 1999; Ungerleider & Mishkin, 1982; Van Essen, Anderson, & Felleman, 1992). For instance, the perception of biological motion involves a wide range of brain regions, in both ventral and dorsal visual pathways (e.g., Grossman et al., 2000), and information of global form can help identifying motion direction (Kuhlmann & Lappe, 2006), and neural dysfunction in the fusiform area impairs the capability to perceive biological motion (Lange et al., 2009). Additionally, static images that have implied motion activate motion selective neurons in both humans (Kourtzi & Kanwisher, 2000) and monkeys (Krekelberg et al., 2003).

However, to our surprise, few if any studies have examined whether the 3-D object structure of a preceding prime stimulus can affect the motion direction of a target SFM stimulus in the absence of overlapping motion signals between the prime and target stimuli. Resolving this question is critical: If the interactions between motion priming and object priming observed in Experiment 2 are due to a strong top-down bias from object selective neurons, then the motion direction perception of an ambiguous helix should be biased by the object structure of a preceding unambiguous helix, even in the absence of motion cues. By contrast, if the interactions between the two modalities of priming are due to the involvement of neurons that are selective to both the object structure and motion direction of SFM stimuli, then the object structure of a preceding unambiguous helix should have no or little impact on the motion direction perception of an ambiguous helix in the absence of motion cue overlap.

To answer these questions, in Experiment 3, we examined whether the perceived rotation direction (around *Y*-axis) of an ambiguous helix (due to the lack of depth cues) can be primed by the object structure of a preceding unambiguous stimulus in the absence of motion cues (i.e., the prime helix was either static or rotating around a different axis, *X*-axis).

### 5.2. Method

To probe the priming of object on motion perception, 3-D helixes with depth cues that were either static or rotating around the *X*-axis (to avoid potential priming due to motion cues) were used as the prime stimuli in Experiment 2. When static, the helix stayed on the screen for about 2 s. When rotating around *X*-axis, the helix rotated around *X*-axis at the speed of 2° per page for 64 pages, and each page stayed on the screen for two frames (about 33.3 ms) – the helix would first rotate 16 pages in one direction, then change rotating direction and rotate another 32 pages, finally it would change direction again and rotate 16 more pages back to the starting point (0°). When the helix was rotating around the *X*-axis, it also gave a strong vivid 3-D perception as rotating around the *Y*-axis (the well known Structure-From-Motion effect). For convenience, later the *X*-rotating helix was named SFXR (Structure-From-X-Rotation) stimuli. The prime and target helixes were presented at the same location on half of the trials, and at the different location (shifted half cycle upward or downward) on the other half of trials.

### 5.3. Results

Similar to what we observed in Experiment 1 and 2, the perception of rotation direction of a single ambiguous helix that rotated around *Y*-axis was ambiguous. Overall, participants perceived that the ambiguous helix rotated in the direction of clockwise on 53% (SEM = 10%) of trials, which was not significantly different from chance level ($p > 0.4$).

In contrast, when an ambiguous helix SFM stimulus was preceded by an unambiguous 3-D helix (static or rotating around *X*-axis), the rotation direction of the ambiguous 3-D helix was primed by the object structure of the preceding unambiguous 3-D helix, but such a priming effect might be weak and sensitive to motion status and position change. To test the prediction, repeated measures analysis of variance (ANOVA) was carried out with the two following factors: position (same vs. different), and prime stimuli type (static vs. SFXR). Significant effects were found for motion direction judgments between position, $F(1,16) = 5.792$, $p < 0.05$, between prime stimuli types, $F(1,16) = 7.411$, $p < 0.05$, and the interactions between the position and prime stimuli type $F(1,16) = 9.692$, $p < 0.01$. Further post hoc analysis indicated that subjects' motion direction perception was significantly affected by the object structure of the prime stimuli when the prime stimuli were SFXR stimuli and were at the same position as the target stimuli ($p = 0.001$), but not significantly for the other three conditions ($p > 0.1$) (Fig. 5). In addition, for the analysis of the response time, there was no significant difference between the positions, $F(1,16) = 0.227$, $p > 0.5$, nor between the prime stimuli types, $F(1,16) = 4.352$, $p = 0.053$, and the interactions between the positions and prime stimuli types, $F(1,16) = 0.082$, $p > 0.5$.

While data from Experiments 1 and 2 revealed a potentially critical role of object structure in motion priming, here in Experiment 3 we observed little or no impact on the motion perception of an ambiguous helix from the object structure of a preceding helix, when there was no overlap in motion cues between the prime and target helixes. These studies are compatible with the fact that there are no direct projections between the ventral lateral occipital (LO) region that is proposed to be shape/object-selective,

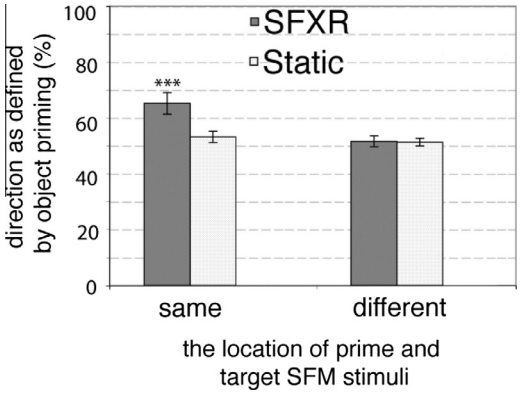


**Fig. 5.** Results of Experiment 3. Subjects were more likely to perceive the ambiguous 3-D helixes rotating in the direction constrained by the object structure of the 3-D helixes prime stimuli, but only when the preceding prime stimuli were SFXR presented at the same location of the target stimuli. ***Represents $p = 0.001$. Error bars represent SEM.

and dorsal MT/V5 region that is proposed to be motion-selective. A recent functional connectivity study utilizing SEM (structural equation modeling) also found little or no functional connectivity between MT and LO (Zhuang et al., 2008). Taken together, results from Experiment 2 and 3 supports an integrated neuronal representation of the motion direction and object structure of an SFM stimulus, in line with a recent report (Pastukhov, Füllekrug, & Braun, 2013).

In addition, the different priming effects with the different prime stimuli and positions raise some important questions. One explanation of the priming effect observed with SFXR prime stimuli that were presented at the same location as the target stimuli is that the priming might be due to priming in low level visual cortex (e.g., V1), which provides a direct input to MT/V5 motion selective neurons. However, this hypothesis is difficult to reconcile with the previous findings that stimuli rotating around the orthogonal axis (e.g., *X*- and *Y*-axis in Experiment 3) do not interact with each other, when tested with motion aftereffect (Nawrot & Blake, 1993) nor with perceptual priming (with a long interval) (Maier et al., 2003). Another alternative interpretation is that the weak priming effect with SFXR prime stimulus at the same position might be due to the illusory depth of the prime SFXR stimulus, as suggested by a previous study that found the rotation direction and depth information might be represented independently, with a stronger priming effect due to depth when the interval was brief as in present study (Pastukhov & Braun, 2013; Pastukhov, Vonau, & Braun, 2012). Therefore, the lack of priming effect under the static image condition would suggest that neural representation of static illusory depth would be different from motion-induced depth perception (Orban, 2011). However, further studies are needed to fully address this question and to examine the interaction between the processing of static and dynamic objects.

## 6. Discussion

Here we examined the interactions between motion priming and object priming in the context of 3-D SFM perception, using a novel SFM stimulus, 3-D helix. The unique feature of 3-D helix is the tangled motion and object perception in the absence of depth cues (Fig. 2), which provides an excellent opportunity to examine the interactions between the two visual pathways, including the interaction between motion perceptual priming and object perceptual priming. In the present study, using a classic prime–target paradigm, we examined whether the motion direction perception of an ambiguous helix could be primed by the motion direction

and/or object structure of a preceding stimulus. Data from Experiment 1 revealed that the perceived motion direction of an ambiguous helix generally followed the unambiguous rotation direction of a preceding cylinder or a set of circles, a classic motion priming effect, however, the motion priming was relatively weaker than those reported in previous studies with a similar brief prime–target interval (e.g., Jiang, Pantle, & Mark, 1998), probably due to the difference in object structure between the prime and target stimuli (Pastukhov, Füllekrug, & Braun, 2013), suggesting a potential important role of object structure in the observations of motion priming. In Experiment 2, we further examined the interactions between motion priming and object priming using 3-D helixes, and found that motion priming was abolished and even overpowered by an incongruent object priming. That is, subjects tended to perceive an ambiguous 3-D helix rotating in the direction defined by the object structure, rather than the motion direction, of the prime unambiguous 3-D helix, even though they were performing a motion direction task on the ambiguous 3-D helixes. The results from Experiment 1 and 2 thus suggested a critical role of object structure in the observations of 3-D rotation priming. However, when there was no overlap in motion cues as in Experiment 3, the object structure alone had no or little effect on biasing the motion direction perception of an ambiguous helix. Taken together, these results revealed a strong interaction between visual inertia of 3-D rotation and object priming, and suggested the motion information of an 3-D SFM stimulus is strongly related to its object structure, that is, the motion and object structure of 3-D SFM stimuli are rather tightly integrated with each other, in line with a recent study (Pastukhov, Füllekrug, & Braun, 2013).

The neural mechanisms underlying motion priming have been investigated using techniques like TMS (Brascamp et al., 2010; Campana, Cowey, & Walsh, 2002), functional magnetic resonance imaging (fMRI) (Ashida et al., 2007; Jiang, Luo, & Parasuraman, 2002), and event-related potentials (Jiang, Luo, & Parasuraman, 2002) in human subjects, and it has been generally in agreement with the idea that motion priming is due to modified neural responses function of MT/V5 neurons, such as residual motion energy (Pinkus & Pantle, 1997). In contrast, object priming has been related to modified neuronal responses at the ventral stream (e.g., Jiang et al., 2007; Kourtzi & Kanwisher, 2001), especially the lateral occipital (LO) region, which has been associated with neural representation of object shapes (Grill-Spector, Kourtzi, & Kanwisher, 2001). However, given there is no known direct anatomic projection between LO and MT/V5 and the weak (near to none) functional connectivity between the two regions (Zhuang et al., 2008), what are the neural mechanisms underlying the *strong* interactions between motion priming and object priming observed in Experiment 2?

During the last two decades, neuroimaging and animal studies have revealed a wide range of brain regions involved in the processing of 3-D dynamic objects (for reviews, see Kourtzi, Krekelberg, & van Wezel, 2008; Orban, 2011; Todd, 2004), including regions in the dorsal (e.g., MT/V5) and ventral (e.g., occipitotemporal region) streams, and parts of the parietal region (e.g., intraparietal sulcus, IPS). While there are general agreements about the early (the computation of motion from V1 to MT/V5) and late (the neural representations of 3-D objects at ventral occipitotemporal region) stages of SFM processing – similar to the field of static object recognition – what is largely unknown is the neural representations and computations at the intermediate levels, i.e., the neural mechanisms transferring 3-D motion to 3-D structure. The location of these potential intermediate neurons are also controversial – studies have proposed candidate regions like superior lateral occipital region (sLO) (Kau et al., 2013; Murray, Olshausen, & Woods, 2003; Peuskens et al., 2004, see also data from patients with lesion, Matheson & McMullen, 2010), ventral part of MT/V5 (or human analogues of hMT+) (Kolster, Peeters, & Orban, 2010; Kourtzi et al., 2002; Mysore et al., 2010; Peuskens et al., 2004), anterior superior temporal polysensory area (STPa) (Anderson & Siegel, 2005), and parts of parietal region (Durand et al., 2007; Kau et al., 2013). To reconcile with these different results, Orban and colleagues have proposed a two-stage model of 3-D SFM processing (Mysore et al., 2010; Orban, 2011), the first step involves the extraction of linear gradients at MT/V5, and the second step involves the extraction of second-order gradients at FST, followed by further projections to regions like STPa, IPS, and sLO (Orban, 2011). Using simultaneously recorded magnetoencephalographic (MEG) and electroencephalographic (EEG) data, the time course within 400 ms of 3-D rotating objects recognition has been reported, where the neural responses in visual cortex V1/V2 → MT/V5 → LO → Temporal Cortex with little overlap in time (Jiang et al., 2008). Interestingly, the activations between MT/V5 and LO were both significantly overlapped with a short transition activation in parietal region, before projecting to ventral temporal region, suggesting parietal regions (e.g. IPS) may serve as a bridge to link motion and shape (Jiang et al., 2008; Orban, 2011). Separated reports from others are consistent with the idea and have found that parietal neurons can accurately encode shape (Sereno & Maunsell, 1998) and motion (Freedman & Assad, 2006) information. Furthermore, lesion to bilateral parietal regions led to miscombining of motion and shape (Bernstein & Robertson, 1998).

Based on these neural mechanisms involved in the processing of 3-D SFM stimuli, here we argue that the region IPS might be the critical region involved in the interaction between the motion priming and object priming: First, the weak motion priming in Experiment 1 and the motion priming under the congruent and incongruent conditions in Experiment 2, especially the abolished or even reversed motion priming under the incongruent condition in Experiment 2 supports the involvement of object structure in the observation of motion priming, suggesting that the interactions between the two priming happens at a stage when or after the object structure has been computed from motion signal, i.e., later than MT/V5 and FST. Secondly, little or no object priming on motion perception in Experiment 3 suggests that the interactions happens at a stage when motion signal is still being relevant, e.g., before the stage of LO (Jiang et al., 2008). Thirdly, neurons in IPS have been shown to be selective to shape (Sereno & Maunsell, 1998) and motion (Freedman & Assad, 2006), and damage to this region led to problems combining motion and shape together (Bernstein & Robertson, 1998), suggesting that IPS might serve as a bridge to link motion and shape (Jiang et al., 2008); Fourthly, using ambiguous stimuli, a recent fMRI study of SFM stimuli and perception repetition found that, while stimuli repetition led to modulations of neuronal responses at visual cortices, the perceptual repetition led to modulations of neuronal responses at parietal region, in addition to visual and frontal cortices (De Jong, Kourtzi, & van Ee, 2012). Based on this hypothesis, we predict that suppressing the IPS region will abolish the impact of object priming, that is, motion priming should be comparable between the congruent and incongruent condition (Fig. 4) if the neuronal responses at the IPS region are suppressed using technique like repetitive TMS (rTMS). In contrast, a recent study found that negative motion aftereffect is shape independent (Pastukhov, Lissner, & Braun, 2014), in contrast to shape-relevant motion priming with a brief (as in the present study) or longer interval (Pastukhov, Füllekrug, & Braun, 2013), but in line with previous studies that suggest motion aftereffect is limited to early visual cortices, such as V1 and MT/V5 (He, Cohen, & Hu, 1998; Huk, Ress, & Heeger, 2001). Therefore we predict that applying rTMS to IPS region would have no impact on motion aftereffect. Interestingly, in supporting our prediction, two rTMS studies have failed to abolish motion aftereffect when rTMS was applied to the parietal region

(Campana, Cowey, & Walsh, 2002; Théoret et al., 2002), and when 2-D motion stimuli were used, applying rTMS to parietal region also had no effect on motion priming (sensory memory with a long interval) (Campana, Cowey, & Walsh, 2002). However, it remains to be tested whether applying rTMS to IPS affect motion aftereffects with 3-D motion. Furthermore, we acknowledge that the interactions could be due to modulations of neurons at other brain regions, such as ventral part of MT/V5, where shape-selective neurons have been proposed (Kolster, Peeters, & Orban, 2010; Kourtzi et al., 2002; Peuskens et al., 2004), or the superior section of LO, which might contain neurons selective to motion and shape (Kau et al., 2013), or STPa, which might integrate the motion and shape information (Anderson & Siegel, 2005). Future studies are necessary to uncover the neural mechanisms underlying the interactions between the motion priming and object priming.

To sum up, using a novel SFM stimulus, 3-D helix, along with a prime–target paradigm, strong interactions between object and motion priming was revealed. The abolished motion priming due to an incongruent object priming and the lack of priming on motion perception with object alone support an integrated neural representation of both the motion and object structure of SFM stimuli. We propose IPS might be a good candidate brain region responsible for the interactions between motion priming and object priming. However, future neuroimaging and electrophysiological studies are needed to examine our hypotheses, and to fulfill the potentials of the current paradigm and novel stimuli in understanding the neural mechanisms underlying 3-D object perception, especially in uncovering the characteristics and the locations of intermediate neurons that compute shape from motion.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2014.08.023.

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